Effect of Tolerance to Insecticides on Substrate Penetration by Formosan Subterranean Termites (Isoptera: Rhinotermitidae)

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ABSTRACT   Seven selected insecticides were applied to three substrates and bioassayed for barrier efficacy and toxicity against the Formosan subterranean termite, *Coptotermes formosanus* Shiraki, originating from colonies that differed in their tolerance to the insecticides. A profound substrate effect was seen with all insecticides tested. Sand was the most difficult substrate to penetrate and caused faster and greater mortality of *C. formosanus.* Increased tolerance in *C. formosanus* was accompanied by a decrease in penetration of treated substrata with chlordane, methoxychlor, chlorpyrifos, and deltamethrin. The opposite was true in the case of permethrin and bendiocarb. More tolerance *C. formosanus* displayed decreased mortality in the presence of chlorpyrifos, deltamethrin, bendiocarb, and fipronil. The opposite was true for permethrin.

KEY WORDS   *Coptotermes formosanus*, termite, insecticide, resistance

TOTAL ECONOMIC LOSS due to termites in the United States was estimated at $1.7 billion per year (Gold et al. 1996a). The Formosan subterranean termite, *Coptotermes formosanus* Shiraki, is native to the Oriental region (Bouillon 1970), but has been introduced into the southern United States where it has become a devastating pest (Su and Tamashiro 1987). Though all currently registered liquid termiticide formulations can be effective when applied as a subsoil treatment, efficacy may vary greatly depending on application rate, soil type, and formulation. Barriers can be breached in the presence of high termite pressure (Jones 1990), gaps (Forschler 1994), inadequate thickness of barrier layer (Ebeling and Pence 1958, Su et al. 1995), insecticide degradation, or if the termiticide is not available to foraging termites for example, due to adsorption onto substrate (Su and Scheffrahn 1990, Gold et al. 1996b).

Sublethal insecticide exposure may be expected to influence insect behavior because most insecticides attack the nervous system resulting in detection by insects, disruption of physiological processes, and behavioral resistance (Haynes 1988, Silverman and Bieman 1993). Assessing the behavioral response of termites to insecticide treated substrates is critical to understanding their effect on termites and termite populations (Su et al. 1982). Further understanding such behavioral traits can enhance pest management strategies and assess the insect's potential for devel-

opment of behavioral resistance, as selection will favor those insects that respond to insecticides in the environment by minimizing their contact with the toxic material (Haynes 1988, Ross and Silverman 1995). Laboratory bioassays have been developed that evaluate the termite's tunneling ability through substrates (Su et al. 1982, 1993, 1995; Tamashiro et al. 1987; Jones 1990; Smith and Rust 1990, Su and Scheffrahn 1990, Grace 1991). Such bioassays provide insight into repellency and effectiveness of an insecticide to provide a barrier necessary for protection of structures. From the standpoint of control, it may be more important to determine whether and to what extent populations differ in their response to insecticides than to determine the basis of a particular behavioral trait (Ross and Cochran 1992).

In this study, seven selected insecticides were applied to three substrates and bioassayed for barrier efficacy and toxicity against *C. formosanus* originating from colonies that differed in their susceptibility to the insecticides.

Materials and Methods

Colonies of *C. formosanus* were obtained from field sites on the grounds of Southern Regional Research Center, United States Department of Agriculture in New Orleans Parrish, LA. *C. formosanus* were collected from bucket traps (Su and Scheffrahn 1986) and maintained on stacked, moistened spruce (*Picea* spp.) slats (10 by 4 by 0.5 cm) in plastic containers (13 by 13 by 4 cm) maintained at ≈100% RH and 26.7 ± 1°C. Termites were identified using soldier keys from

Table 1. Insecticide susceptibility among *Coptotermes formosanus* colonies (Osbrink et al. 2001)

Insecticide (μg/cm^2)	Colony	n	Slope $\pm$ SE[a]	LT$_{50}$ (95% FL) (min)	LT$_{90}$ (95% FL) (min)	χ^2	Tolerance ratio LT$_{90}$ (95% CI)
Chlordane	FW-S9	40	11.3 $\pm$ 1.8b	10.2 (7.4–12.8)	16.5 (13.1–29.2)	2.1	1.0
(630.65)	FW-S7	40	8.9 $\pm$ 0.7b	61.1 (58.7–63.4)	85.2 (81.2–90.6)	6.2	6.3 (5.6–7.1)
Methoxychlor	FW-S19	40	14.4 $\pm$ 1.0a	153.8 (151.0–156.5)	188.9 (183.8–195.3)	3.2	1.0
(5260.0)	FW-S9	40	6.5 $\pm$ 1.1b	211.1 (197.6–229.1)	333.0 (283.5–458.7)	0.9	1.2 (1.0–1.4)
Chlorpyrifos	FW-S9	40	8.4 $\pm$ 1.3a	11.8 (10.9–12.6)	16.8 (15.5–19.0)	0.0	1.0
(526.13)	FW-S7	40	28.1 $\pm$ 4.2b	35.9 (34.9–36.8)	39.8 (38.5–42)	0.6	2.4 (2.1–2.7)
Permethrin	FW-S9	40	6.5 $\pm$ 1.0a	23.6 (16.5–27.4)	37.1 (31.2–68.1)	5.1	1.0
(5.26)	FW-S19	40	4.0 $\pm$ 0.3d	83.5 (78.7–89.3)	176.2 (153.9–211.7)	7.9	4.8 (3.7–6.1)
Deltamethrin	FW-S9	40	13.6 $\pm$ 1.3abc	21.0 (19.8–22.5)	27.9 (25.5–32.8)	0.4	1.0
(0.053)	FW-S7	40	2.9 $\pm$ 0.4e	165.8 (150.2–191.8)	456.6 (346.7–708.5)	5.0	16.0 (11.9–21.5)
Bendiocarb	FW-S19	40	11.5 $\pm$ 1.7a	19.8 (18.7–20.9)	25.6 (23.7–29.0)	0.7	1.0
(2.63)	FW-S9	40	8.9 $\pm$ 1.1a	23.2 (19.6–26.7)	32.4 (27.8–47.8)	6.0	1.3 (1.1–1.5)
Fipronil	FW-S7	40	12.4 $\pm$ 0.8b	189.3 (185.9–193.1)	240.1 (234.3–247.5)	4.8	1.0
(630.65)	FW-S19	40	10.4 $\pm$ 0.6b	248.7 (243.0–255.2)	330.2 (315.5–349.3)	19.0[b]	1.4 (1.3–1.5)

[a] Slopes followed by the same letter indicate the hypothesis that the lines are parallel cannot be rejected when $P > 0.05$.

[b] Chi-square exceeds tabular $P = 0.05$ value.

Scheffrahn and Su (1994) and Su et al. (1997b). All termites were tested within 30 d of their collection.

Termite colonies were previously tested for their sensitivity to insecticides (Osbrink et al. 2001) by exposing them to a filter paper surface treated with known amount of toxicant as modified from Su et al. (1987). Based on the study by Osbrink et al. (2001), three colonies (S7, S9, and S19) with the highest and lowest tolerance to each of seven insecticides, were evaluated for their response to three different substrates treated with each of seven different toxicants in glass tube assays. LT$_{50}$s, LT$_{90}$s, slopes, and tolerance ratios for *C. formosanus* workers of these three colonies are reported in Table 1 (Osbrink et al. 2001). Toxicants used in this study were technical grade except for chlordane. Name and purity are as follows: Chlordane, 45% Chlordane Concentrate Termite Control with 50% petroleum distillate and 5% inert ingredients manufactured by Federal Chemical (Indianapolis, IN); methoxychlor, 99.0%; chlorpyrifos, 99.0%; permethrin, 99.5%; deltamethrin, 99.2%; bendiocarb, 76.0%; and fipronil, 96%. These chemicals were selected to represent different classes of insecticides.

Bioassays were conducted in glass tubes (1.4 cm i.d. by 15 cm high) with 5-cm segments of a centrally placed substrate contained on each end with 1 cm of 7% agar (Su and Scheffrahn 1990). Two wooden sticks and a strip of filter paper were placed into the 5-cm space at the bottom of the vertically placed tube. Fifty third-instar or greater workers, as determined by size, and five soldiers were placed in the bottom space of four similarly prepared glass tubes (replicates). Filter paper was placed in the top void of the tube. Tubes were sealed at both ends with plastic caps and aluminum foil modified with pinholes for aeration. All substrates were treated with insecticide at 5 ppm (weight active ingredient/weight substrate) in acetone and the acetone was then allowed to evaporate. Pilot studies found 5 ppm an acceptable rate that showed differences between termite colonies and substrates. Substrate moisture was adjusted to 15% by volume. Control substrates were moistened but not treated with insecticide. Substrates tested were sand (Stan-dard Sand and Silica Company, Davenport, FL), potting soil (Scotts, Marysville, OH), and potting soil and kaolin clay (Great Lakes Clay and Supply Company, Carpenterville, IL) mixed 50:50 by volume, hereafter referred to as clay. Organic matter in potting soil was ≈7% as determined by Walkly-Black (Jackson 1958) wet digestion method (Louisiana State University Soil Testing Laboratory, Baton Rouge, LA) with 3.3, 66.7, and 30.0% sand, silt, and clay, respectively. Substrates were chosen because of their different affinities for absorption and adsorption of insecticides (Harris 1972). All substrates were slightly acidic (≈pH 6), as determined qualitatively with pH paper. Samples were held at 26.7 $\pm$ 1°C and ≈100% RH. Termite penetration (0–5 cm) was evaluated and termite mortality was estimated up to 30 d at 5-d intervals. Absolute termite mortality was determined at 30 d.

Cumulative penetration and mortality (mean percentage and SD) were calculated for each treatment. Treatments from the same time and toxicant were compared using analysis of variance (ANOVA) following transformation by the arcsine square root proportion penetration or mortality. Means were separated using an unprotected Fisher least significant difference (LSD) multiple range test ($P = 0.05$), (SAS Institute 1990). Actual percent penetration or mortality is reported in Tables 2 and 3.

Results and Discussion

Masses of *C. formosanus* workers (mean $\pm$ SD, mg) of those colonies tested are as follows: S7 = 2.52 $\pm$ 0.1, S19 = 2.33 $\pm$ 0.1, S9 = 3.70 $\pm$ 0.1 ($F = 3.033$; df = 2, 27; $P < 0.065$)

Significantly greater mortality occurred with chlordane treated sand (Table 2; Fig. 1) compared with the other substrates beginning at 10 d ($F = 22.39$; df = 11, 36; $P < 0.0001$) and through 25 d ($F = 4.29$; df = 11, 36; $P < 0.0004$). Only in treated sand did 100% mortality occur. Sand retains more of the toxicant on the particle's surface than the other substrates (Harris 1972). Of the three substrates, only treated sand was not completely penetrated (Table 3; Fig. 1) by either

Table 2. Cumulative % mortality of *C. formosanus* in tube test

Treatment colony	Substrate	% mortality (mean ± SE)[a] days						
		1	5	10	15	20	25	30
Chlordane								
S9	Sand	0b	1.7 ± 1.9abc	100.0a	100.0a	100.0a	100.0a	100.0a
S7	Sand	0b	10.8 ± 6.9a	91.7 ± 16.7a	100.0a	100.0a	100.0a	100.0a
S9	Soil	0.8 ± 1.7b	2.5 ± 3.2abc	2.5 ± 3.2bc	10.0 ± 2.7bc	16.7 ± 4.7cd	57.5 ± 29.9bc	70.8 ± 34.4AB
S7	Soil	0.8 ± 1.7b	0.8 ± 1.7abc	3.3 ± 0bc	10.0 ± 2.7bc	12.5 ± 3.2cd	31.7 ± 15.5cd	53.3 ± 32.6BC
S9	Clay	2.5 ± 1.7a	2.5 ± 1.7abc	2.5 ± 3.2bc	5.8 ± 9.6c	11.7 ± 5.8cd	45.8 ± 10.7bcd	58.3 ± 28.9AB
S7	Clay	0b	7.5 ± 15.0abc	2.5 ± 1.7bc	8.3 ± 1.9bc	13.3 ± 6.1cd	55.0 ± 21.5bcd	74.2 ± 20.6AB
Untreated								
S9	Sand	0b	0c	0.8 ± 1.7c	1.7 ± 1.9c	59.2 ± 47.2b	80.0 ± 40.0abc	80.0 ± 40.0AB
S7	Sand	0b	0c	1.7 ± 3.3c	1.7 ± 3.3c	9.2 ± 4.2d	9.2 ± 4.2d	9.2 ± 4.2D
S9	Soil	0b	10.0 ± 20.0abc	20.0 ± 17.9b	39.2 ± 43.2b	47.5 ± 36.4bc	68.3 ± 36.7abc	83.3 ± 33.3AB
S7	Soil	0b	0.8 ± 1.7bc	15.8 ± 29.5bc	25.8 ± 49.5bc	35.8 ± 43.6bcd	60.0 ± 46.3bc	60.0 ± 46.3AB
S9	Clay	0b	11.7 ± 13.5ab	14.2 ± 22.2bc	27.5 ± 48.6bc	32.5 ± 45.3bcd	55.8 ± 49.8bc	55.8 ± 49.8BC
S7	Clay	0b	9.2 ± 16.2abc	9.2 ± 16.2bc	9.2 ± 16.2bc	13.3 ± 14.1cd	13.3 ± 14.1d	13.3 ± 14.1CD
Methoxychlor								
S9	Sand	0a	9.2 ± 63.ab	9.2 ± 6.3abc	9.2 ± 6.3ab	32.5 ± 45.1abc	37.5 ± 41.8ab	80.0 ± 38.3ab
S19	Sand	0a	11.7 ± 8.8ab	11.7 ± 8.8abc	54.2 ± 53.4ab	77.5 ± 45.0a	80.0 ± 40.0a	100.0a
S9	Soil	0a	5.0 ± 4.3ab	5.0 ± 4.3bc	14.2 ± 7.9ab	18.3 ± 3.3bc	45.0 ± 15.5ab	86.7 ± 20.6ab
S19	Soil	0a	2.5 ± 3.2b	5.8 ± 3.2abc	7.5 ± 3.2ab	11.7 ± 1.9c	16.7 ± 2.7b	83.3 ± 33.3ab
S9	Clay	0a	4.2 ± 4.2ab	4.2 ± 4.2bc	8.3 ± 1.9ab	9.2 ± 1.7c	15.8 ± 4.2b	83.3 ± 33.3ab
S19	Clay	0a	24.2 ± 28.3a	29.2 ± 30.6a	67.5 ± 45.6a	75.8 ± 48.3ab	75.8 ± 48.3a	75.8 ± 48.3ab
Untreated								
S9	Sand	0a	0b	0.8 ± 1.7c	1.7 ± 1.9b	59.2 ± 47.2abc	80.0 ± 40.0a	83.3 ± 33.3ab
S19	Sand	0a	0b	7.5 ± 12.9bc	50.0 ± 57.7ab	56.7 ± 50.3abc	76.7 ± 46.7a	76.7 ± 46.7ab
S9	Soil	0a	10.0 ± 20.0ab	20.0 ± 17.9abc	39.2 ± 43.2ab	47.5 ± 36.4abc	68.3 ± 36.7ab	83.3 ± 33.3ab
S19	Soil	0a	1.7 ± 3.3b	5.8 ± 11.7bc	25.0 ± 50.0ab	34.2 ± 44.3abc	34.2 ± 44.3ab	34.2 ± 44.3b
S9	Clay	0a	11.7 ± 13.5ab	31.7 ± 45.8a	31.7 ± 45.8ab	32.5 ± 45.3abc	55.8 ± 49.8ab	55.8 ± 49.8ab
S19	Clay	0a	17.7 ± 33.3ab	12.5 ± 20.8abc	27.5 ± 48.6ab	28.3 ± 48.0abc	29.2 ± 47.3ab	29.2 ± 47.3b
Chlorpyrifos								
S7	Sand	5.0 ± 7.9b	85.8 ± 24.1a	92.5 ± 15.0a	100.0a	100.0a	100.0a	100.0a
S9	Sand	12.5 ± 11.4a	93.3 ± 13.3a	100.0a	100.0a	100.0a	100.0a	100.0a
S7	Soil	0c	0.8 ± 1.7c	14.2 ± 5.7b	18.3 ± 8.8bcd	20.2 ± 9.0bc	45.0 ± 38.0bc	45.0 ± 38.0bc
S9	Soil	0c	29.2 ± 47.4b	29.2 ± 47.4bc	35.0 ± 35.0bc	47.5 ± 37.0bc	99.2 ± 1.7a	99.2 ± 1.7a
S7	Clay	0c	1.7 ± 1.9c	2.5 ± 1.7bcd	3.3 ± 0.0bcd	7.5 ± 4.2c	10.0 ± 5.4c	10.0 ± 5.4c
S9	Clay	0c	2.5 ± 5.0c	5.0 ± 4.3bcd	12.5 ± 8.3bcd	41.7 ± 39.1bc	86.7 ± 16.3b	86.7 ± 16.3ab
Untreated								
S7	Sand	0c	0c	0d	1.7 ± 3.3d	9.2 ± 4.2c	9.2 ± 4.2c	9.2 ± 4.2c
S9	Sand	0c	0c	0.8 ± 1.7cd	1.7 ± 1.9d	59.2 ± 47.2ab	80.0 ± 40.0ab	80.0 ± 40.0ab
S7	Soil	0c	0.8 ± 1.7c	15.8 ± 29.5bcd	25.8 ± 49.5bcd	35.8 ± 43.6bc	60.0 ± 46.3ab	60.0 ± 46.3ab
S9	Soil	0c	10.0 ± 20.0bc	20.0 ± 17.9b	39.2 ± 43.2b	47.5 ± 36.4bc	68.3 ± 36.7ab	83.3 ± 33.3ab
S7	Clay	0c	9.2 ± 16.2bc	9.2 ± 16.2bcd	9.2 ± 16.2bcd	13.3 ± 14.1c	13.3 ± 14.1c	13.3 ± 14.1c
S9	Clay	0c	11.7 ± 13.5bc	14.2 ± 22.2bcd	27.5 ± 48.6bcd	32.5 ± 45.3bc	55.8 ± 49.8ab	55.8 ± 49.8b
Permethrin								
S9	Sand	0b	1.7 ± 1.9a	8.3 ± 8.8abc	18.3 ± 11.1ab	18.3 ± 11.1b	66.7 ± 26.1ab	93.3 ± 13.3a
S19	Sand	3.3 ± 2.7a	3.3 ± 2.7a	2.5 ± 3.2bc	70.8 ± 34.4a	85.0 ± 17.5a	96.7 ± 6.7a	96.7 ± 6.7a
S9	Soil	0b	0a	0c	5.0 ± 5.8b	7.5 ± 5.0b	45.0 ± 37.6ab	51.7 ± 32.9abc
S19	Soil	0b	0a	0c	25.8 ± 49.5b	27.5 ± 48.6b	38.3 ± 41.7ab	100.0a
S9	Clay	0b	3.3 ± 3.9a	4.2 ± 3.2bc	26.7 ± 44.5b	27.5 ± 43.9ab	63.3 ± 43.1ab	83.3 ± 33.3ab
S19	Clay	0b	1.7 ± 3.3a	8.3 ± 16.7bc	35.0 ± 44.4b	35.8 ± 43.7ab	35.8 ± 43.7ab	35.8 ± 43.7bc
Untreated								
S9	Sand	0b	0a	0.8 ± 1.7bc	1.7 ± 1.9b	59.2 ± 47.2ab	80.0 ± 40.0ab	83.3 ± 33.3ab
S19	Sand	0b	0a	7.5 ± 12.9bc	50.0 ± 57.7a	56.7 ± 50.3ab	76.7 ± 46.7a	76.7 ± 46.7ab
S9	Soil	0b	10.0 ± 20.0a	20.2 ± 17.9ab	39.2 ± 43.2b	47.5 ± 36.4ab	68.3 ± 36.7ab	83.3 ± 33.3ab
S19	Soil	0b	1.7 ± 3.3a	5.8 ± 11.7bc	25.0 ± 50.0ab	34.2 ± 44.3ab	34.2 ± 44.3b	34.2 ± 44.3bc
S9	Clay	0b	11.7 ± 13.5a	31.7 ± 45.8a	31.7 ± 45.8ab	32.5 ± 45.3ab	55.8 ± 49.8ab	55.8 ± 49.8abc
S19	Clay	0b	16.7 ± 33.3a	12.5 ± 20.8abc	27.5 ± 48.6ab	28.3 ± 48.0ab	29.2 ± 47.3b	29.2 ± 47.3c
Deltamethrin								
S7	Sand	0b	1.2 ± 3.3b	6.7 ± 4.7abc	6.7 ± 4.7b	10.0 ± 4.7c	10.0 ± 4.7c	10.0 ± 4.7c
S9	Sand	0b	28.3 ± 48.2a	31.7 ± 45.9a	31.7 ± 45.9ab	59.2 ± 47.2a	79.2 ± 41.7a	83.3 ± 33.3a
S7	Soil	0.8 ± 1.7b	0.8 ± 1.7	5.0 ± 3.3abc	13.3 ± 61.ab	13.3 ± 6.1abc	13.3 ± 6.1bc	60.0 ± 46.3abc
S9	Soil	0.8 ± 1.7b	0.8 ± 1.7	8.3 ± 6.4abc	14.2 ± 5.7ab	14.2 ± 5.7abc	14.2 ± 5.7bc	83.3 ± 33.3a
S7	Clay	0b	4.2 ± 8.3ab	6.7 ± 6.7abc	13.3 ± 9.8ab	13.3 ± 9.8bc	13.3 ± 9.8bc	13.3 ± 9.8bc
S9	Clay	2.5 ± 1.7a	2.5 ± 1.7ab	9.2 ± 5.7abc	57.5 ± 49.1a	57.5 ± 49.1ab	57.5 ± 49.1ab	58.3 ± 46.4abc
Untreated								
S7	Sand	0b	0b	0c	1.7 ± 3.3b	9.2 ± 4.2c	9.2 ± 4.2c	9.2 ± 4.2c
S9	Sand	0b	0b	0.8 ± 1.7bc	1.7 ± 1.9b	59.2 ± 47.2a	80.0 ± 40.0a	80.0 ± 40.0a
S7	Soil	0b	0.8 ± 1.7bc	1.7 ± 1.9b	59.2 ± 47.2a	80.0 ± 40.0a	80.0 ± 40.0a	
S7	Soil	0b	0.8 ± 1.7b	15.8 ± 29.5abc	25.8 ± 49.5ab	35.8 ± 43.6a	60.0 ± 46.3a	60.0 ± 46.3ab
S9	Soil	0b	10.0 ± 20.0ab	20.0 ± 17.9ab	39.2 ± 43.2ab	47.5 ± 36.4abc	68.3 ± 36.7a	83.3 ± 33.3a
S7	Clay	0b	9.2 ± 16.2ab	9.2 ± 16.2b	9.2 ± 16.2b	13.3 ± 14.1bc	13.3 ± 14.1c	13.3 ± 14.1bc
S9	Clay	0b	11.7 ± 13.5ab	14.2 ± 22.2abc	27.5 ± 48.6ab	32.5 ± 45.3abc	55.8 ± 49.8abc	55.8 ± 49.8abc

(continued)

Table 2. Continued.

Treatment colony	Substrate	% mortality (mean ± SE)[a] days						
		1	5	10	15	20	25	30
Bendiocarb								
S9	Sand	0a	6.7 ± 2.7a	8.3 ± 4.3bcd	13.3 ± 13.3b	16.7 ± 14.1b	20.0 ± 14.1c	42.5 ± 40.3bc
S19	Sand	0a	28.3 ± 47.9a	54.2 ± 49.3a	75.0 ± 45.7a	75.8 ± 44.0a	100.0a	100.0a
S9	Soil	0a	3.3 ± 2.7ab	41.7 ± 40.5ab	45.0 ± 40.1ab	60.8 ± 33.2ab	60.8 ± 33.2abc	83.3 ± 33.3ab
S19	Soil	0a	10.0 ± 6.1ab	25.8 ± 16.6abcd	41.7 ± 17.5ab	49.2 ± 16.6ab	65.0 ± 31.6abc	80.0 ± 29.9abc
S9	Clay	0a	2.5 ± 5.0b	8.3 ± 4.3bcd	10.8 ± 3.2b	42.5 ± 38.4ab	65.8 ± 40.6abc	88.3 ± 13.7ab
S19	Clay	0a	10.0 ± 2.7ab	15.0 ± 8.8abcd	18.3 ± 5.8ab	19.2 ± 5.0ab	44.2 ± 37.5bc	44.2 ± 37.5bc
Untreated								
S9	Sand	0a	0b	0.8 ± 1.7d	1.7 ± 1.9b	59.2 ± 47.2ab	80.0 ± 40.0ab	83.3 ± 33.3ab
S19	Sand	0a	0b	7.5 ± 112.9cd	50.0 ± 57.7ab	56.7 ± 50.3ab	76.7 ± 46.7ab	76.7 ± 46.7abc
S9	Soil	0a	10.0 ± 20.0ab	20.0 ± 17.9abcd	39.2 ± 43.2ab	47.5 ± 36.4ab	68.3 ± 36.7abc	83.3 ± 33.3ab
S19	Soil	0a	1.7 ± 3.3b	5.8 ± 11.7cd	25.0 ± 50.0b	34.2 ± 44.3ab	34.2 ± 44.3bc	34.2 ± 44.3bc
S9	Clay	0a	11.7 ± 13.5ab	31.7 ± 45.8abc	31.7 ± 45.8ab	32.5 ± 45.3ab	55.8 ± 49.8abc	55.8 ± 49.8abc
S19	Clay	0a	16.7 ± 33.3ab	12.5 ± 20.8bcd	27.5 ± 48.6ab	28.3 ± 48.0ab	29.2 ± 47.3bc	29.2 ± 47.3c
Ripronil								
S7	Sand	0a	86.7 ± 26.7a	100.0a	100.0a	100.0a	100.0a	100.0a
S19	Sand	0a	90.8 ± 18.3a	100.0a	100.0a	100.0a	100.0a	100.0a
S7	Soil	0a	38.3 ± 37.4b	100.0a	100.0a	100.0a	100.0a	100.0a
S19	Soil	0.8 ± 1.7a	8.3 ± 10.0bc	95.0 ± 6.4a	95.0 ± 6.4ab	100.0a	100.0a	100.0a
S7	Clay	0a	80.8 ± 27.5a	100.0a	100.0a	100.0a	100.0a	100.0a
S19	Clay	0.8 ± 1.7a	37.5 ± 31.6b	100.0a	100.0a	100.0a	100.0a	100.0a
Untreated								
S7	Sand	0a	0c	0b	1.7 ± 3.3d	9.2 ± 4.2c	9.2 ± 4.2c	9.2 ± 4.2d
S19	Sand	0a	0c	7.5 ± 12.9b	50.0 ± 57.7bc	56.7 ± 50.3b	76.7 ± 46.7ab	76.7 ± 46.7ab
S7	Soil	0a	0.8 ± 1.7c	15.8 ± 29.5b	25.8 ± 49.5cd	35.8 ± 43.6bc	60.0 ± 46.3bc	60.0 ± 46.3bc
S19	Soil	0a	1.7 ± 3.3c	7.5 ± 11.0b	27.5 ± 48.4cd	34.2 ± 44.3bc	34.2 ± 44.3cd	34.2 ± 44.3cd
S7	Clay	0a	9.2 ± 16.2c	10.0 ± 15.9b	10.0 ± 15.9cd	13.3 ± 14.1c	13.3 ± 14.1d	13.3 ± 14.1d
S19	Clay	0a	16.7 ± 33.3bc	18.3 ± 32.4b	26.7 ± 49.0cd	26.7 ± 49.0bc	27.5 ± 48.4cd	27.5 ± 48.4cd

Means within a column of each toxicant and untreated with the same letter are not significantly different (LSD, $P = 0.05$).

[a] Fifty workers (≥3rd instar) and five soldier per replicate with four replicates.

colony, with significantly less penetration of chlordane treated sand than soil or clay from 15 d ($F = 10.16$; df = 11, 36; $P < 0.0001$) and beyond. Similar substrate effects were seen by Smith and Rust (1993), who found chlordane killed *Reticulitermes* spp. at >1 ppm, with increased concentrations of organic matter (cellulose) causing toxicity and effective repellency to decrease. Osmun (1956) also found chlordane was more active against *Reticulitermes* spp. with sandier soils at 5 ppm. Colony S7 (6.3 times more tolerant, Table 1) penetrated all chlordane treated substrates significantly less than colony S9 at 5 d ($F = 8.48$; df = 11, 36; $P < 0.0001$) and clay at 10 d ($F = 7.76$; df = 11, 36; $P < 0.0001$) even though colony S9 had significantly greater mortality than S7 in untreated sand beginning at 20 d ($F = 6.66$; df = 11, 36; $P < 0.0001$). The more tolerant colony (S7) penetrated chlordane treated substrates more slowly. Smith (1979) found chlordane toxic and repellent at 5 ppm in sandy loam to *Reticulitermes* spp. Tamashiro et al. (1987) also found that sand treated with chlordane was the most difficult substrate for *C. formosanus* to penetrate. In contrast, Su et al. (1982) found chlordane did not repel *C. formosanus* at 100 ppm in agar. The interaction of chlordane with the highly organic agar may account for this response difference.

Methoxychlor (a DDT analog) treated substrates caused 100% mortality only with colony S19 in sand at 30 d (Table 2; Fig. 1). Hetrick (1957) found that it took methoxychlor 3 d at 1,000 ppm to kill *Reticulitermes* spp. in sandy soil. Methoxychlor treated sand was not completely penetrated (<90%) by either colony S9 or S19 (Table 3; Fig. 1). Colony S19 penetrated significantly farther (Table 3; Fig. 1) than colony S9 (1.2 times but not significantly more tolerant, Table 1) in treated sand at 5 and 15 d ($F = 5.39$; df = 11, 36; $P < 0.0001$ and $F = 4.65$; df = 11, 36; $P < 0.0002$, respectively). Complete penetration of treated soil and clay by both colonies occurred at 5 d. Incorporation of methoxychlor into organic substances could explain the substrate effects (Soma and Soma 1989). The more tolerant colony (S9) generally penetrated the methoxychlor treated substrates more slowly

In chlorpyrifos treated sand, colony S7 (2.4 times more tolerant, Table 1) sustained significantly less mortality than S9 (Table 2; Fig. 2) at 1 d ($F = 6.92$; df = 11, 36; $P < 0.0001$, but not at later days. Colony S7 also had significantly less mortality than S9 at 25 d in treated soil ($t = 2.733$; df = 1, 6; $P = 0.034$) and clay ($t = 5.958$; df = 1, 6; $P = 0.001$) as well as at 30 d in treated soil ($t = 2.733$; df = 1, 6; $P = 0.034$) and clay ($t = 5.958$; df = 1, 6; $P = 0.001$). Treated sand caused significantly higher mortality and lower penetration compared with the other substrates (Tables 2 and 3, LSD; $P = 0.05$). Chlorpyrifos was reported by others also to kill *Reticulitermes* spp. at >1 ppm with decreased efficacy in the presence of increased organic matter (Smith and Rust 1990, 1993), or increased soil or clay (Henderson et al. 1998, Forschler and Townsend 1996, Gold et al. 1996b). Chlorpyrifos treated sand was penetrated significantly less by the more tolerant colony (Table 3; Fig. 2) at 5 d ($t = 2.976$;

Table 3. Substrate % penetration of *C. formosanus* in tube test

Treatment colony	Substrate	% penetration (mean ± SD)[a] days						
		1	5	10	15	20	25	30
Chlordane								
S9	Sand	47.9 ± 22.2bcd	71.0 ± 21.3b	74.5 ± 19.1bc	74.5 ± 19.1b	74.5 ± 19.1b	74.5 ± 19.1b	74.5 ± 19.1b
S7	Sand	37.5 ± 9.6bcd	40.0 ± 11.6c	65.0 ± 10.0c	65.0 ± 10.0b	65.0 ± 10.0b	65.0 ± 10.0b	65.0 ± 10.0c
S9	Soil	35.0 ± 17.bcd	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S7	Soil	20.0 ± 11.6d	60.0 ± 33.7bc	100.0a	100.0a	100.0a	100.0a	100.0a
S9	Clay	67.5 ± 12.6bcd	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S7	Clay	35.0 ± 10.0cd	75.5 ± 30.2b	75.5 ± 30.2b	91.0 ± 18.0a	91.0 ± 18.0a	100.0a	100.0a
Untreated						100.0a		
S9	Sand	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S7	Sand	75.5 ± 40.2ab	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S9	Soil	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S7	Soil	41.0 ± 45.8bcd	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S9	Clay	66.0 ± 47.2bc	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S7	Clay	49.5 ± 38.5bcd	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
Methoxychlor								
S9	Sand	24.0 ± 22.2c	45.0 ± 37.9b	72.5 ± 32.0b	72.5 ± 32.0b	87.0 ± 26.0a	87.0 ± 26.0a	87.0 ± 26.0a
S19	Sand	45.0 ± 37.6bc	86.0 ± 28.0b	86.0 ± 28.0b	86.0 ± 28.0a	86.0 ± 28.0a	86.0 ± 28.0a	86.0 ± 28.0a
S9	Soil	39.0 ± 43.9bc	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S19	Soil	47.0 ± 37.9bc	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S9	Clay	79.0 ± 42.0ab	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S19	Clay	85.0 ± 30.0ab	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
Untreated								
S9	Sand	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S19	Sand	71.0 ± 47.9abc	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S9	Soil	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S19	Soil	81.5 ± 37.0ab	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S9	Clay	66.0 ± 47.2abc	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S19	Clay	79.0 ± 21.1abc	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
Chlorpyrifos								
S7	Sand	2.5 ± 5.0d	8.0 ± 3.7d	8.0 ± 3.7c	8.0 ± 3.7c	8.0 ± 3.7c	8.0 ± 3.7c	8.0 ± 3.7c
S9	Sand	20.2 ± 21.6cd	30.0 ± 16.3c	30.0 ± 16.3b	30.0 ± 16.3b	30.0 ± 16.3b	30.0 ± 16.3b	30.0 ± 16.3b
S7	Soil	7.5 ± 9.6d	64.0 ± 31.1b	87.5 ± 25.0a	100.0a	100.0a	100.0a	100.0a
S9	Soil	35.0 ± 31.1bcd	95.5 ± 9.0a	95.5 ± 9.0a	100.0a	100.0a	100.0a	100.0a
S7	Clay	40.0 ± 45.5bcd	95.0 ± 10.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S9	Clay	67.5 ± 29.9abc	91.0 ± 18.0a	100.0a	100.0a	100.0a	100.0a	100.0a
Untreated								
S7	Sand	75.5 ± 40.2ab	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S9	Sand	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S7	Soil	41.0 ± 45.8bcd	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S9	Soil	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S7	Clay	49.5 ± 38.5bcd	100.0a	100.0a	100.0a	100.0a	100.0a	
S9	Clay	66.0 ± 47.2abc	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
Permethrin								
S9	Sand	8.0 ± 9.2d	14.0 ± 9.5c	14.0 ± 9.5b	14.0 ± 9.5b	20.0 ± 16.3b	20.0 ± 16.3b	20.0 ± 16.3b
S19	Sand	2.0 ± 4.0d	18.5 ± 8.7c	18.5 ± 8.7b	23.0 ± 17.2b	34.5 ± 23.4b	34.5 ± 23.4b	34.5 ± 23.4b
S9	Soil	24.5 ± 9.6cd	83.0 ± 22.7b	100.0a	100.0a	100.0a	100.0a	100.0a
S19	Soil	32.0 ± 9.4bcd	95.0 ± 10.0ab	100.0a	100.0a	100.0a	100.0a	100.0a
S9	Clay	72.5 ± 19.9ab	90.0 ± 20.0ab	90.0 ± 20.0a	90.0 ± 20.0a	90.0 ± 20.0a	90.0 ± 20.0a	90.0 ± 20.0a
S19	Clay	84.0 ± 19.6a	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
Untreated								
S9	Sand	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S19	Sand	71.0 ± 47.9ab	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S9	Soil	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S19	Soil	81.5 ± 37.0a	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S9	Clay	66.0 ± 47.2abc	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S19	Clay	79.0 ± 21.1a	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
Deltamethrin								
S7	Sand	8.0 ± 7.1e	13.0 ± 3.5cd	13.0 ± 3.5d	13.0 ± 4.8c	13.0 ± 4.8c	14.0 ± 4.9c	14.0 ± 4.9c
S9	Sand	4.0 ± 3.7e	10.0 ± 6.7d	38.5 ± 41.9c	41.0 ± 39.9b	41.0 ± 39.9b	43.0 ± 38.7b	43.0 ± 38.7b
S7	Soil	28.5 ± 7.6cde	39.5 ± 16.4c	35.0 ± 17.3cd	57.5 ± 31.0b	57.5 ± 31.0b	57.5 ± 31.0b	57.5 ± 31.0b
S9	Soil	58.5 ± 8.7bcd	80.0 ± 28.3ab	100.0a	100.0a	100.0a	100.0a	100.0a
S7	Clay	18.5 ± 14.0de	70.5 ± 37.4b	78.5 ± 27.0b	87.5 ± 25.0a	90.0 ± 20.0a	90.0 ± 20.0a	90.0 ± 20.0a
S9	Clay	61.0 ± 29.5bc	80.0 ± 28.3ab	100.0a	100.0a	100.0a	100.0a	100.0a
Untreated								
S7	Sand	75.5 ± 40.2ab	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S9	Sand	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S7	Soil	41.0 ± 45.8bcde	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S9	Soil	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S7	Clay	49.5 ± 38.5bcde	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S9	Clay	66.0 ± 47.2abc	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a

Table 3. Continued.

Treatment colony	Substrate	% penetration (mean ± SD)[a] days						
		1	5	10	15	20	25	30
Bendiocarb								
S9	Sand	7.0 ± 6.8e	16.5 ± 4.7c	18.0 ± 9.1b	20.5 ± 8.1b	22.5 ± 6.0b	22.5 ± 6.0b	24.5 ± 4.1c
S19	Sand	2.0 ± 2.8e	15.0 ± 4.2c	15.0 ± 4.2b	15.0 ± 4.2b	16.5 ± 4.7b	16.5 ± 47.b	16.5 ± 4.7c
S9	Soil	20.0 ± 16.3de	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S19	Soil	4.5 ± 5.8e	47.0 ± 7.4b	90.0 ± 20.0a	90.0 ± 20.0a	90.0 ± 20.0a	90.0 ± 20.0a	90.0 ± 20.0b
S9	Clay	62.5 ± 32.6bcd	89.0 ± 22.0a	89.0 ± 22.0a	89.0 ± 22.0a	100.0a	100.0a	100.0a
S19	Clay	23.5 ± 17.5cde	95.0 ± 10.0a	100.0a	100.0a	100.0a	100.0a	100.0a
Untreated								
S9	Sand	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S19	Sand	71.0 ± 47.9ab	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S9	Soil	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S19	Soil	81.5 ± 37.0ab	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S9	Clay	66.6 ± 47.2abc	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S19	Clay	79.0 ± 21.1ab	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
Fipronil								
S7	Sand	23.0 ± 5.3bc	26.5 ± 5.0c	29.5 ± 7.6cd	29.5 ± 7.6cd	29.5 ± 7.6cd	29.5 ± 7.6cd	29.5 ± 7.6cd
S19	Sand	17.0 ± 16.8c	27.0 ± 18.1c	28.0 ± 15.8cd	28.0 ± 15.8cd	28.0 ± 15.8cd	28.0 ± 15.8cd	28.0 ± 15.8cd
S7	Soil	19.0 ± 14.1bc	27.0 ± 18.1c	27.0 ± 18.1c	27.0 ± 18.1d	27.0 ± 18.1d	27.0 ± 18.1d	27.0 ± 18.1d
S19	Soil	14.5 ± 6.0c	28.0 ± 9.2c	30.0 ± 7.6cd	30.0 ± 7.6cd	30.0 ± 7.6cd	30.0 ± 7.6cd	30.0 ± 7.6cd
S7	Clay	16.5 ± 12.4c	50.0 ± 35.6b	55.0 ± 33.2b	55.0 ± 33.2b	55.0 ± 33.2b	55.0 ± 33.2b	55.0 ± 33.2b
S19	Clay	31.5 ± 14.5b	42.5 ± 3.05bc	47.5 ± 3.0bc	47.5 ± 3.0bc	47.5 ± 3.0bc	47.5 ± 3.0bc	47.5 ± 3.0bc
Untreated								
S7	Sand	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S19	Sand	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S7	Soil	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S19	Soil	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S7	Clay	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a
S19	Clay	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a	100.0a

Means within a column for each toxicant and untreated with the same letter are not significantly different (LSD, $P = 0.05$).
[a] Fifty workers (≥3rd instar) and five soldier per replicate with four replicates.

df = 1, 6; $P = 0.025$) and beyond. Treated soil was also penetrated numerically less by S7 at 1 and 5 d. Thus, the more tolerant colony (S7) penetrated the chlorpyrifos treated substrates more slowly and had lower mortality. Chlorpyrifos was found to be degraded to ≈5 ppm in <5 yr in various soils and still cause mortality in *Reticulitermes* spp. (Kard et al. 1989, Gold et al. 1996b, Kard 2001). Su et al. (1997a) found field populations of *C. formosanus* penetrated chlorpyrifos treated sand from 0 to 5 cm at 10 ppm. Gahlhoff and Koehler (2001) found that *Reticulitermes* sp. would penetrate chlorpyrifos treated sand at 5 ppm with ≈50% mortality, but not at 50 ppm.

Termite mortality in permethrin treated substrates was not significantly greater than in untreated substrates (Table 2; Fig. 2) except for colony S19 (4.8 times more tolerant, Table 1) in sand at 1 d ($F = 6.00$; df = 11, 36; $P < 0.0001$) and soil at 30 d ($t = 2.972$; df = 1, 6; $P = 0.025$). Su et al. (1982) demonstrated that termites often avoid repellent toxicants and survive. In permethrin-treated sand, colony S19 had consistently higher mortality than the less tolerant colony (S9), with significant differences at 1 d ($t = 2.818$; df = 1, 6; $P = 0.030$) and 20 d ($t = 4.703$; df = 1, 6; $P = 0.003$). Penetration was 100% by 5 d in all untreated substrates (Table 3; Fig. 2). Permethrin treated sand was not completely penetrated by either colony, with colony S9 (less tolerant) penetrating numerically less than colony S19 at 5 d ($t = 0.699$; df = 1, 6; $P = 0.511$) to 30 d ($t = 1.017$; df = 1, 6; $P = 0.348$). Treated sand was penetrated significantly less than the other substrates

at 5 d ($F = 25.82$; df = 11, 36; $P < 0.0001$) and beyond. With permethrin treated substrates, the more tolerant colony tended to penetrate more rapidly and sustain higher mortality. Notably, in field studies by Gold et al. (1996b), permethrin degraded to ≈5 ppm in <5 yr and still not penetrated by *Reticulitermes* spp.; Kard et al. (1989) saw permethrin lose its effectiveness in <5 yr. Henderson et al. (1998) found some mortality with permethrin at 5 ppm against *C. formosanus.* Smith and Rust (1990) found that permethrin killed termites in soil plate tests at 1 ppm. Smith (1979) found sandy loam treated with permethrin as repellent at 5 ppm. *C. formosanus* penetration of permethrin treated sand was stopped in the laboratory test at 1 ppm (Su et al. 1997a, Su and Scheffrahn 1990) but only at >10 ppm against field populations (Su et al. 1997a). Tamashiro et al. (1987) also found that sand was most difficult to penetrate compared with other substrates treated with permethrin.

Deltamethrin treated sand consistently killed fewer termites from S7 (16 times more tolerant, Table 1), possessing the largest insecticide tolerance difference in this study, than colony S9. These mortality differences between colonies in sand had significant unprotected LSDs at 5 d ($t = 1.101$; df = 1, 6; $P = 0.313$, 20 d ($t = 2.074$; df = 1, 6; $P = 0.083$), and significant t values at 25 d ($t = 3.342$; df = 1, 6; $P = 0.016$), and 30 d ($t = 4.177$; df = 1, 6; $P = 0.006$) (Table 2; Fig. 3). Mortality results for colony S9 were confounded by the presence of high SD and elevated control mortality beginning at 20 d. Colony S9, while more suscep-
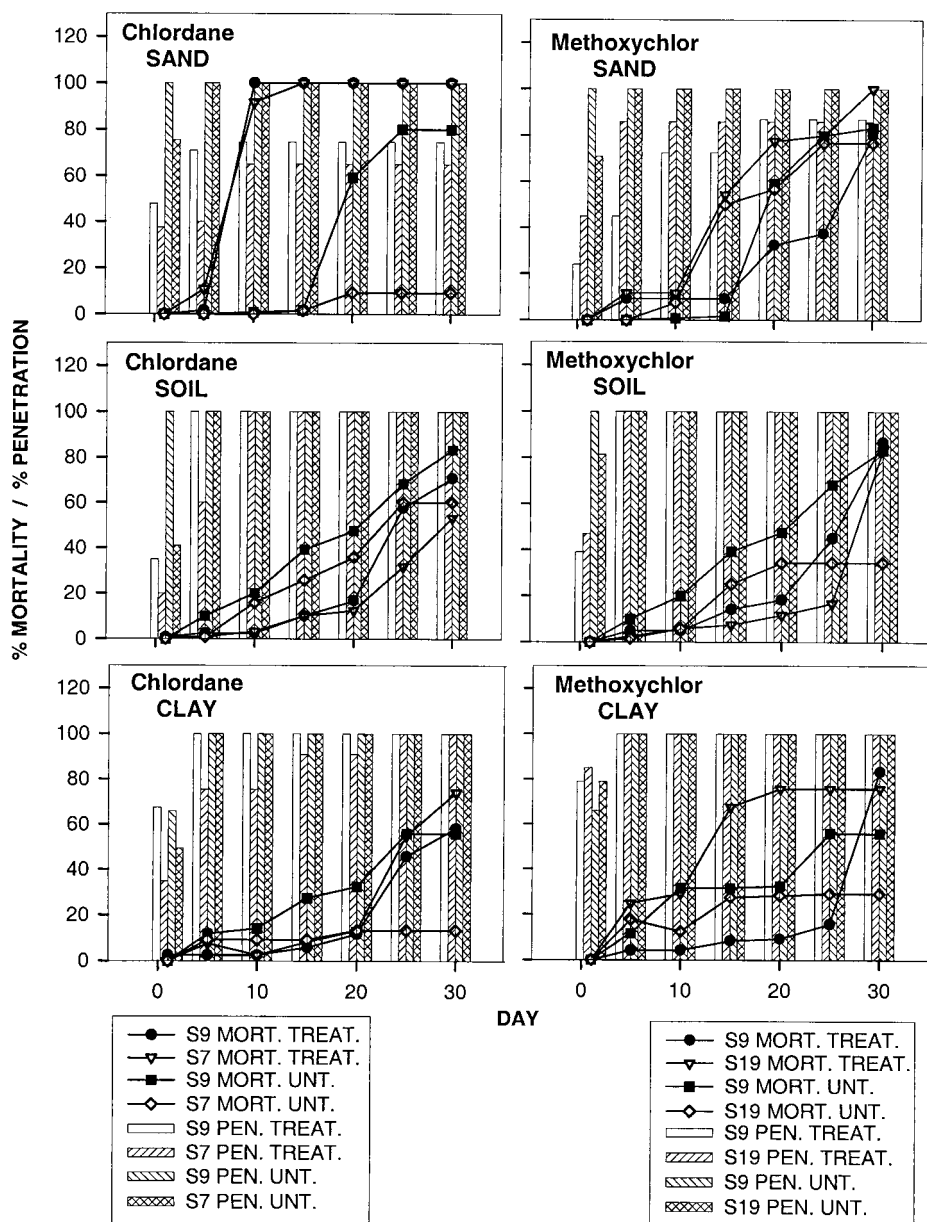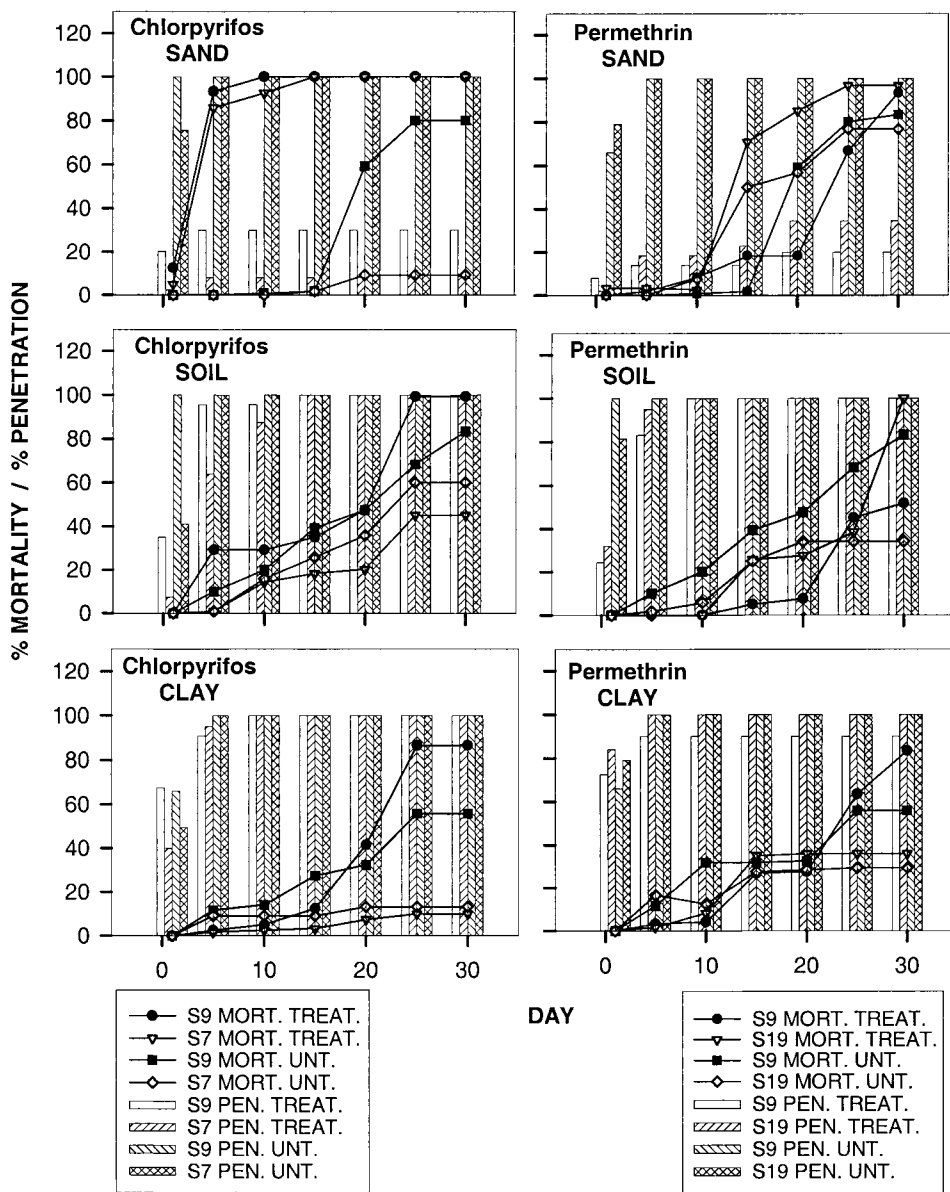
Fig. 1. Cumulative percent mortality and penetration of *C. formosanus* with three substrates treated with 5 ppm chlordane or methoxychlor.

tible, consistently penetrated all three deltamethrin treated substrates more rapidly and completely than colony S7 (Table 3; Fig. 3). Penetration differences between colonies were most pronounced in soil with significant *t* values at 5 d ($t = 2.476$; df = 1, 6; $P = 0.048$), 10 d ($t = 7.514$; df = 1, 6; $P < 0.001$), 15 d ($t = 2.742$; df = 1, 6; $P = 0.034$), 20 d ($t = 2.742$; df = 1, 6; $P = 0.034$), 25 d ($t = 2.742$; df = 1, 6; $P = 0.034$), and 30 d ($t = 2.742$; df = 1, 6; $P = 0.034$). Susceptible colony S9 also penetrated treated clay significantly further at 1 d than S7 ($t = 2.603$; df = 1, 6; $P = 0.040$). Deltamethrin soil and clay treated substrates were com-

pletely penetrated only by colony S9. Su and Scheffrahn (1990) found deltamethrin stopped penetration of *C. formosanus* at ≈6 ppm and Kard (2001) reported an initial treatment of ≈25 ppm deltamethrin provided several years of an effective barrier at different field sites.

Bendiocarb treated sand caused significantly greater mortality in colony S19 than colony S9 (1.3 times more tolerant, Table 1) at 10 d ($F = 2.05$; df = 11, 36; $P < 0.0515$) and beyond. Neither colony completely penetrated the treated sand barrier. The treated soil barrier also was not completely penetrated

Fig. 2. Cumulative percent mortality and penetration of *C. formosanus* with three substrates treated with 5 ppm chlorpyrifos or permethrin.

by colony S19. With treated soil, the more tolerant colony (S9) penetrated more rapidly than S19, significant only at 5 d ($t = 14.324$; df $= 1, 6$; $P = 0.001$).

Fipronil treated substrates all caused 100% mortality by 10 d except for colony S19 (1.4 times more tolerant, Table 1) in soil in which 100% mortality occurred at 20 d (Table 2; Fig. 4). Mortality at 5 d was greater for the more susceptible colony (S7) in treated soil and significantly greater in treated clay ($F = 12.97$; df $= 11$, 36; $P < 0.0001$). Treated sand caused significantly more rapid mortality than the other substrates ($F = 12.97$; df $= 11$; $P < 0.0001$). None of the fipronil treated substrates were completely penetrated by ei-

ther colony (Table 3; Fig. 4). Colony S7 penetrated treated clay significantly further than either colony penetrated treated sand or soil at 5 d ($F = 36.39$; df $= 11$, 36; $P < 0.0001$) and beyond. Kard (2001) found fipronil in concrete slab and ground board test good for 6 yr at ≈ 15 ppm.

A profound substrate effect was observed with all insecticide treatments. Treated sand was the most difficult substrate to penetrate and caused faster and greater mortality of *C. formosanus*. Sand retains more of the toxicant on the particle's surface than the other substrates (Harris 1972). As the colloidal fraction of the substrate increases, as in soil and clay, surface area
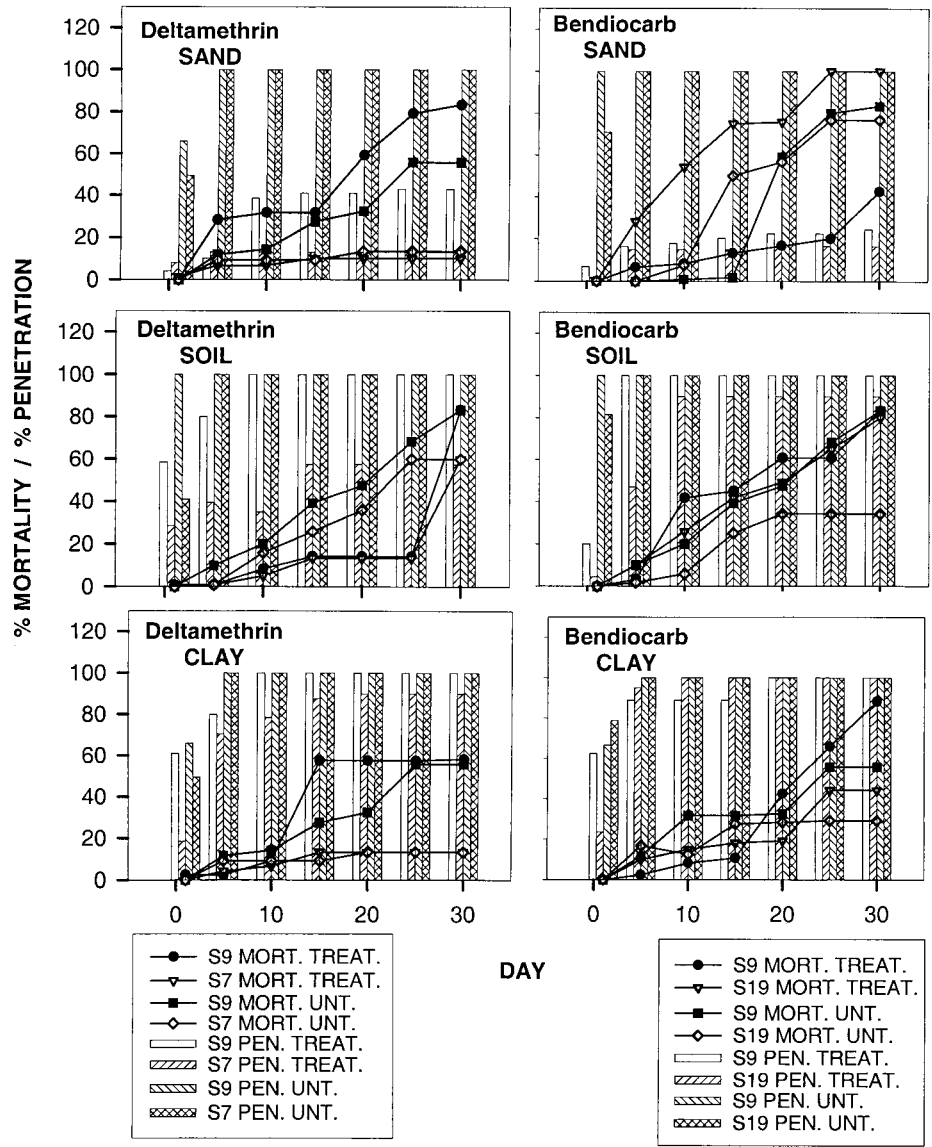
Fig. 3. Cumulative percent mortality and penetration of *C. formosanus* with three substrates treated with 5 ppm deltamethrin or bendiocarb.

and chemical binding sites increase greatly. This substrate effect is consistent with the findings of other researchers (Osmun 1956; Tamashiro et al. 1987; Smith and Rust 1990, 1993; Forschler and Townsend 1996; Gold et al. 1996b). A paucity of information exists on the basic nature of interactions between pesticide and soil colloids. Adsorption is a benchmark property needed to predict biological activity in soil. Certainly the pesticide chemical character of the molecule, size, shape, conformation, configuration, polarity, polarizability, pH, charge distribution, and water solubility are important factors. With regards to availability of pesticide for uptake by the target organism, behavior of the chemical at the soil-air-water interface will interact with an almost infinite number of environmental combinations of almost infinite variables in soil properties (Saltzamn and Yaron 1986). Main factors considered as relevant for the adsorption-desorption of pesticides in soils are the nature and properties of the organic and inorganic soil colloids, the chemical and physiochemical characteristics of pesticides, and the features of the soil environment (Saltzamn and Yaron 1986). For hydrophobic insecticide adsorbates mostly used in termite control, humified organic matter is one of the most active adsorbents in soil and deactivates pesticides through adsorption mechanisms such as Vander Waals forces, hydrogen bonding, and hydrophobic bonding.
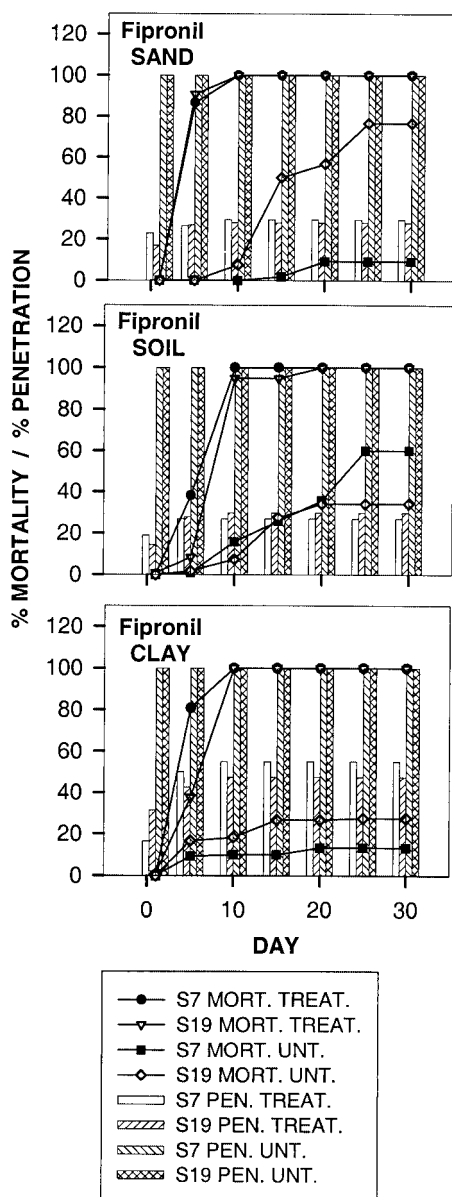
Fig. 4. Cumulative percent mortality and penetration of *C. formosanus* with three substrates treated with 5 ppm fipronil.

though the importance of organic matter in pesticide adsorption has been well established, the properties of the organic colloids relevant for adsorption have not yet been thoroughly characterized. Clays by themselves, or by interaction with the soil organic matter, can significantly affect the uptake of nonionic molecules such as termiticides (Mingelgrin and Gerstl 1983). Clays and soil minerals are also rather heterogeneous and many types of interactions may control adsorption on them. In addition, to their tremendous surface area, clays are also well know as potential catalyzers of various types of reactions of the adsorbed molecules such as hydrolysis of phosphate ester bonds (Mingelgrin and Saltzman 1979).

Increased insecticide tolerance of *C. formosanus* was accompanied by a decrease in penetration of treated substrata with chlordane, methoxychlor, chlorpyrifos, and deltamethrin. The opposite was true of permethrin and bendiocarb. More tolerant *C. formosanus* colonies displayed decreased mortality in the presence of chlorpyrifos, deltamethrin, bendiocarb, and fipronil. The opposite was true for permethrin. The avoidance of treated substrate with chlordane, methoxychlor, chlorpyrifos, and deltamethrin is similar to behavior seen in resistant strains of the house fly, *Musca domestica* L., that showed a correlated behavioral resistance in their avoidance of malathion (Fay et al. 1958, Kilpatrick and Schoof 1958). Physiologically, resistant strains of the house fly also showed a correlated behavioristic resistance in their avoidance of baits (Fay et al. 1958). German cockroaches, *Blattella germanica* (L.), also avoided a toxicant by development of an aversion to glucose (Silverman and Bieman 1993, Ross and Silverman 1995). Behavioral resistance is indicated by reduced contact with a toxic material (Haynes 1988). Widespread use of insecticides has resulted in behavioral changes in insect populations (Bret and Ross 1985). Localized populations of German cockroach have developed many different combinations of behavioral modification and physiological/biochemical resistance (Ross 1993). Behavior is the final outcome of a sequence of neurophysiological events involving sensory neurons, interneurons, motor neurons, and finally muscular contractions. Detection and avoidance of insecticide in German cockroaches, as indicated by repellency, was attributed to chemosensory responses (Bret and Ross 1985). A source of differences in behavior among strains is alteration in sensory perception of insecticides perhaps advantageous to the insect's survival such as behavioral resistance (Ross and Cochran 1992). Use of insecticides usage has selected for altered behavior as well as physiological and biochemical resistance in insect populations (Ross 1993). Variation in insecticide induced behavior is likely the result of differences in the way in which populations adapt to localized conditions (Ross 1993). Resistance and repellency may interact to increase survival of resistant strain exposed to insecticide (Rust and Reierson 1978).

Termites more tolerant to permethrin and bendiocarb had increased penetration of treated substrates. Different insecticides are likely to have different types

(Leenheer and Ahlrichs 1971). Variation in adsorption as affected by the type of material to which insecticides are applied is of great practical importance because it is related to toxicity and repellency. The majority of termite-substrate laboratory bioassays are conducted with sand, which maximizes pesticide performance. Results of such bioassays should be interpreted cautiously. Organic matter and mineral colloid relationships, rather than isolated parameters, must be considered in the assessment of pesticide adsorption by soils (Saltzman and Yaron 1986). Al-

of behavioral effects in the same species (Haynes 1988). Resistant German cockroaches were slower to avoid the pyrethroid cyfluthrin (Ross 1993) and did not avoid cyfluthrin or cypermethrin the way susceptible cockroaches did (Ross and Cochran 1992). Increased penetrations of more tolerant termites into the bendiocarb (carbamate) treated substrates are similar to results of decreased sensitivity to another carbamate, propoxur, observed by Bret and Ross (1985, 1986) as a reduction in behavioral response by resistant German cockroaches. Increased resistance to the carbamate propoxure also caused decreased sensitivity in the behavioral response in German cockroaches (Bret and Ross 1986).

Decreased mortality in the presence of chlorpyrifos, deltamethrin, bendiocarb, and fipronil is consistent with the advantage obtained through surviving selection pressure. Chlorpyrifos killed less then half the resistant *B. germanica* when compared with a susceptible strain (Rust et at. 1993). Chlorpyrifos also killed less resistant German cockroaches in choice tests (Ross and Cochran 1992). Increased susceptibility and irritability to malathion in a laboratory strain of German cockroaches was associated with a reduced ability to detoxify the pesticide (Bret and Ross 1985). Assessing the potential effect of insecticide-induced behavior on the control of insect pests is complicated by genetically controlled differences in the population's behavior (Haynes 1988). Possibilities of strain or individual colony differences in response to insecticide deposits have received little attention (Ross and Cochran 1992). Behavioral studies are needed to enhance pest management strategies and assess an insect's potential for development of behavioral resistance (Haynes 1988). Further assessment of this phenomenon is needed in the context of field studies such as Su et al. (1997a), where termite pressures are orders of magnitude greater than in laboratory studies.

Acknowledgments

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